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PALEONTOLOGY.—*Some primitive fossil pelecypods and their possible significance.* H. E. VOKES, Johns Hopkins University.

In a recent stimualting paper on "Primitive Fossil Gastropods and Their Bearing on Gastropod Classification" Dr. J. Brookes Knight (1952) presents convincing evidence to support his thesis that the Cambrian gastropods *Scenella* Billings and *Helcionella* Grabau and Shimer and their apparent immediate descendants in the Ordovician, with representatives into the Devonian, are very close to the ancestral gastropod type. All have simple cap- or spoon-shaped shells with the apex subcentral to anterior in position. Muscle scars have been observed in 6[1] of the 12 genera that he has grouped under the family Triblidiidae Pilsbry; these scars are discreet and arranged in bilaterally symmetrical pairs within the margins of the shell. Knight includes the Triblidiidae plus certain related but somewhat more advanced families and the Polyplacophora in a separate subclass of the Gastropoda for which he reintroduces Lankester's term *Isopleura*, defining it as follows (p. 45): "Gastropods that retain throughout life both in the shell and in the soft anatomy the primitive bilateral symmetry of the class. They are entirely marine and always rare. They first appear in the fossil record in Lower Cambrian rocks and carry through to the present. They probably originated in pre-Cambrian time."

The paired muscle scars are exceptionally well preserved in the genera *Archaeophiala* Koken in Perner 1903, from the Upper Ordovician of Sweden, and *Triblidium* Lindström 1880, from the Silurian of Gotland, Sweden. Both were earlier well-figured by Knight (1941, pl. 3, fig. 3a, b; and pl. 3, figs. 6a, d, respectively), and an accurate drawing of *Archaeophiala* is included in the recent paper (1952, pl. 1, figs. 3a, b) [see Fig. 1]. Concerning *Archaeophiala*, Knight (1952, p. 27) says:

> The scars are strongly pigmented and for that reason are unusually sharp and clear. These scars are 12 in number and are arranged in a ring deep within the margin of the shell. Two of the scars are larger than the others and are made up of three parts. These tripartite scars, which occur at one end, may be regarded as compound and perhaps as representing the scars of three muscles each. The other 10 scars are simple and probably are the scars of single muscles. These 12 (or 16) scars are in bilaterally symmetrical pairs. The pair of large compound scars lies at the end toward which the apex lies and very nearly closes the circle at that end. The scars of the other five pairs follow symmetrically on either side until the circle is nearly closed at the other end. There is a line of much fainter, unpigmented scars outside of the principal ring. The six (or eight) pairs of pigmented scars were probably points of attachment for symmetrically paired muscles connecting the shell to the foot. One can hardly guess what function was served by the muscles that made the more obscure scars outside those of the main circle but these shadow scars appear to be characteristic of the group.
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> Two exceedingly important inferences are suggested by the scars of *Archaeophiala*. The first inference is that the soft anatomy was bilaterally symmetrical throughout, that is to say the animal had not undergone torsion. This is an inference primarily from the complete bilateral symmetry of the paired muscle scars, supported by the lack of an area between the scars at either end for a pallial cavity. The second inference is that the end that has the large compound muscle scars and toward which the apex lies is anterior. This follows as probable from a corollary to the principle of cephalization to the effect that

[1] Subsequent to the completion of this manuscript, Rasetti (Journ. Pal. **28** (1): 59, pl. 12, figs. 5–8. 1954) has described similarly paired scars in a Middle Cambrian species of *Scenella*, thus confirming Knight's deductions as to the position of this genus. This brings to seven the number of triblidiid genera in which such scars have been observed.

'heteronomous segmentation is an expression of cephalization.'

The muscle scars of *Triblidium* are "virtually identical" with those of *Archaeophiala* (Knight, 1952, p. 27, ftn. 10).

Recently the writer came across some notes prepared while reading Neumayr's classic "Beitrage zu einer morphologischen Eintheilung der Bivalven" (1891). In this work the author discusses certain unusual types of musculature to be observed on early Paleozoic pelecypods, stating in part (p. 754–755, freely translated):

> Further peculiarities must be observed in the muscle structure. In many geologically young forms there are three small accessory muscle impressions, in the interior of the valve close to the beak, which serve the foot muscle. This characteristic becomes more and more emphasized in the Paleozoic forms: as a representative for this I have proposed the genus, or rather, subgenus *Myoplusia*. In *Leda bilunata* these accessory muscle impressions are very highly developed (Barr. Tab. 270, f. 1, 6, 10); in one of them [tab. 270, fig. 6—see fig. 2, this paper], between the posterior adductor and the beak, there are two additional muscle impressions which equal the first in size and strength; two more-elongated impressions that extend from the beak downwards. It is, of course, a question if the very highly developed muscle structure that corresponds to such scars was only intended for the foot, but there is no evidence as to the function of this muscular structure concentrated around the beak. It becomes still more confusing in the very peculiar genus *Anuscula* from the lower Silurian [Ordovician] of Bohemia.[2]
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> This is an oval form with a small number of teeth under a slightly protruding beak. The pear-shaped adductor muscles begin as very narrow, close to the beak and extend along the margin to almost the center of the height of the shell. The space between both adductors is filled with 4 or 5 elongated smaller muscle impressions in the region around the beak. It is not yet possible to explain these arrangements or those of *Myoplusia*. As *Anuscula* includes the geologically oldest forms that we know, we must give special attention to its peculiar characteristics and keep the possibility in mind that this muscle arrangement may have been widely developed in the still older Cambrian bivalves.

[2] Barrande, J.: *Syst. Silurien de Boheme* **6**: 31. Barrande used a number of Bohemian words as generic names and, apparently uncertain as to their validity, also gave latin "translations." The species referred to *Anuscula* by Neumayr were actually described under the name *Babinka*, a term that Neumayr erroneously indicates as equivalent to *Matercula* Barrande, which term Barrande uses as an alternative for his *Maminka*.

An examination of the figures of Barrande (1881, pls. 266, 269–272) reveals that there are a number of species referred by Barrande to *Babinka*, *Nucula*, and *Leda* that show multiple paired muscle scars under the beaks between the adductors. At least three different types of muscle modification may be observed in the species figured on these plates. In *Babinka* [*Anuscula*] (Figs. 6, 7) there are elongate, superficially pear-shaped anterior and posterior adductors that are prolonged dorsally toward the umbo. Between them, under the umbo, are 4 or 5 smaller elongate scars. According to Barrande the number of these supplementary scars varies within the species (see Barrande, pl. 266, figs. 6 and 15; also Figs. 6, 7, this paper). The adductor scars are 10 to 12 mm in length and approximately 2 mm wide, the supplementary scars are 5 to 6 mm long in *Babinka prima* Barrande, a species which averages 24 mm in length.

The scars of *Myoplusia* (Fig. 2)[3] have been well described by Neumayr. Those of the third group (Figs. 3, 4, 5) are well shown in *"Nucula" amica* Barrande, a species referred by Pfab (1934, p. 232) to his genus *Praeleda*. Here, as shown in Barrande (pl. 271, figs. 6, 8), there are three smaller elongate scars between the adductors, and a fourth dorsal to, and parallel with, the posterior adductor. In addition to these there are what appear to be smaller scars ventral to the three scars between the adductors, one below each of them, which are curiously reminiscent of the "fainter, unpigmented scars" described by Knight. The specimen figured by Pfab (1934, pl. 3, fig. 5) seems to retain part of the shell and the scars are not well shown. In sketches (pl. 1, figs. 16a, 16b) Pfab indicates, however, that the essentially pear-shaped anterior adductor of Barrande's

[3] Pfab (1934, pl. 2, fig. 11) gives a photographic figure of the original specimen of this illustration. He refers to it as *Ctenodonta* (*Ctenodonta*) *bilunata bilunata*, describing a new variety as *Ct.* (*Ct.*) *bilunata perdentata* Pfab. He makes the latter the "type" of his "Gruppe des Schlosstypus V" which includes only these two forms. He does not mention *Myoplusia* Neumayr except in the synonymy of *bilunata bilunata*.

The muscle scars, which show well in his figure, are not discussed beyond the statement that they are prominent.

figure is bi-partite, the larger portion being considered as the adductor, a smaller adumbonal portion being indicated as a pedal muscle scar; it may well have functioned as a diductor. In addition Pfab gives illustrations of *Praeleda compar* (Barrande) (1934, p. 232, pl. 1, fig. 22, pl. 3, figs. 1–3) and of *P. contrastans* (Barrande) (1934, p. 233, pl. 1, fig. 23, pl. 3, figs. 4, 7–9) of which pl. 3, figs. 2 (*compar*) and 4 (*contrastans*) show traces of musculature on the umbo similar to that shown in Barrande's figures of his "*Nucula*" *amica*. There are, thus, a number of species in the group three type that show multiple muscle scars.

The striking similarity between the general pattern of the muscle scars exhibited by these early pelecypods and those known in the triblidiid gastropods is such that, considering their approximate contemporaneity and low stratigraphic position, the writer is led to feel that conclusions of biologic significance may be drawn from it. Knight was of the opinion that the triblidiid gastropods were close to the ancestral stock from which the class was derived, and his restoration of a generalized sceneliid with the muscle scars of *Archaeophiala* (Knight, 1952, figs. 5a, b) is but little modified from that of the hypothetical primitive mollusk radical as restored by Pelseneer (1906) and others. If such was the case then it might be safe to assume that the type of musculature observed in the triblidiids was essentially similar to that to be found in the ancestral form. If this assumption be allowed, then the types of muscle scars to be observed in the early pelecypods mentioned above may be interpreted as primitive modifications from the same ancestral condition, and therefore, these pelecypods are close to the ancestral type and occupy an ancestral position in the phylogeny of the *Pelecypoda* as a whole.

If this be correct it may be concluded that the adductor muscles of the pelecypods are derived from discreet pairs of the ancestral musculature, the anterior adductor being an enlargement of the anterior pair, and the posterior adductors representing an enlargement of one of the more posterior pairs. In most of the forms it would seem that the posterior pair of muscles was enlarged to form the adductor, but if the figures of "*Nucula*" *amica* Barrande are correctly interpreted, it is evident that, in this form at least, it was the penultimate pair that was so modified.

In some respects, at least, it is tempting to consider that the type of musculature found in "*Leda*" *bilunata* reflects its closeness to the ancestral type, rather than the posterior elongation of the shell. That species, however, was said by Barrande to have come from "Sterbohol-d4." The strata at this locality are correlated by later authors with the upper Caradoc of the standard Ordovician section, approximately late Utica in terms of the North American classification. "*Nucula*" *amica* was described from the same horizon at "Butowitz," while *Babinka prima* was described from

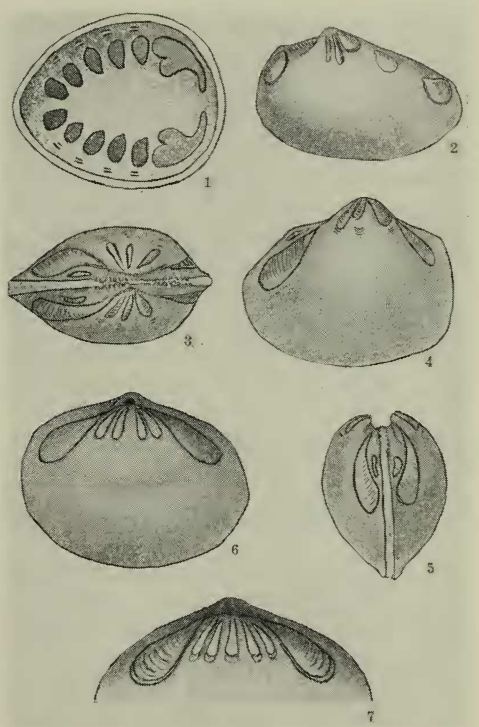

Fig. 1.—*Archiophiala antiquissima* (Hisinger), after Knight, 1952, pl. 1, fig. 3b. Fig. 2.—"*Leda*" *bilunata* Barrande; after Barrande, 1881, pl. 270, fig. 6. Figs. 3–5.—"*Nucula*" *amica* Barrande, three views of the same specimen, after Barrande, 1881, pl. 271, figs. 6–8. Figs. 6–7.—*Babinka* [*Anuscula*] *prima* Barrande, after Barrande, 1881, pl. 266, figs. 11 and 15, respectively. (All except figure 7 approximately natural size.)

"Wosek-d1," strata that are now considered as U. Arenig or L. Llandeilo (Chazyan) in age. It has also been reported as occurring in strata of Upper Tremadoc and L. Arenig age in the Herault area of southern France. (Thoral, 1935, p. 162, pl. 13, figs. 4a, b, 5a, b).

It is clear, therefore, that the symmetrical *Babinka prima* type is the older. However, it seems quite unlikely that either the hinge types, nor the peculiar muscle patterns that mark "*Leda*" *bilunata* and "*Nucula*" *amica* could have been derived from those to be observed in *Babinka prima*. Two alternatives may be suggested: (1) that all three were derived from presently unknown pelecypod ancestors, or (2) that these early pelecypod types were polyphyletic in origin, and were separately derived from the prepelecypod ancestral stock. While it must be admitted that the known geologic occurrence of the species in question tempts one to place weight on the second possibility, it must be kept in mind that conditions of fossil preservation adequate for the observation of such details as the muscle scars are so rarely met with that it may well be that all three types of observed patterns represent offshoots from a common, and as yet unknown, stock.

In conclusion, therefore, it is the opinion of the writer that the muscle scars shown by these Ordovician pelecypods can be shown to be close to those exhibited by primitive gastropods, as figured by Knight; that they therefore may be interpreted as reflecting the musculature present in the ancestral stock from which the Pelecypoda were derived; and, in view of their similarity to the gastropod condition, that they afford evidence confirmatory to the arguments of Knight that the gastropods of the family Triblidiidae are close to the ancestral stock in the gastropod line. Further, they suggest that the adductor muscles of the Pelecypoda are derived from discreet pairs of the ancestral musculature, rather than from the union of multiple pairs.

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MYCOLOGY.—Aphanomyces euteiches *from pea roots and* "Aphanomyces euteiches *P. F. 2.*"

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The original account (Jones and Drechsler, 1925) of my *Aphanomyces euteiches* was based entirely on the saprolegniaceous parasite that occurs during wet seasons as a causal agent of serious root rot in garden peas (*Pisum sativum* L.). Soon after the account was published Linford (1927) reported having found oospores typical of the fungus also in diseased roots of narrow-leaved vetch (*Vicia angustifolia* L.) seedlings as well as in diseased seedlings of alfalfa (*Medicago sativa* L.) and sweet clover (*Melilotus alba* Desr.). He further observed several varieties of sweet peas (*Lathyrus odoratus* L.) greatly weakened from spontaneous attack by the parasite, and in inoculation trials successfully infected nine additional leguminous species. Mainly because of similarities shown by oospores found in their decaying roots he considered four nonleguminous plants including barley (*Hordeum vulgare* L.) and oats (*Avena sativa* L.) subject to invasion by *A. euteiches*. Subsequent study of a culture isolated by Linford from an oat root, however, revealed distinctive morphological and developmental features; wherefore it was used as type material of a separate species, *A.*